THE DIGESTION OF WOOD BY TEREDO NAVALIS

BY

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CONTENTS

INTRODUCTION

Ever since the classical investigations of *Teredo* by Sellius in 1733, it has been debated periodically whether or not the destructive boring mollusks of this group derive any nutriment from the wood which they so effectively perforate. Sellius himself discussed the question (p. 108) without arriving at a definite conclusion. Reimarus (1773, pp. 55 ff.) expressed a negative opinion, which was shared by Home (1814, p. 373), who examined wood particles removed from the bodies of the animals and thought them to be unchanged by the digestive fluids. Baumhauer (1866, p. 19) states unreservedly that *Teredo* bores in wood, not for nutriment, but solely to secure a protected dwelling. Most recent writers, such as Sigerfoos (1908, p. 218), Moll (1914, p. 257), and Calman (1919, p. 12), although considering plankton the principal food of the organisms, admit the possibility that some nourishment may be derived from the wood. Bartsch, however, in a recent monograph (1922) inclines to the earlier view of non-utilization of the wood particles as food, suggesting (p. 4) with apparent seriousness that "the shipworm may simply indulge in a partial meal of this kind to have the comfortable feeling of a copious repast."

BIOLOGICAL CONSIDERATIONS

The arguments against utilization of the wood as food are several and varied. Certain near relatives of *Teredo* (*Pholas, Zirphaea,* and *Saxicava*) bore for protection only, in such substances as sandstone, limestone, shale, marl, and gneiss—materials which cannot be supposed to yield them any nourishment; these indigestible borings may even be found in considerable quantities in the digestive tract of the rock borers (Calman, 1919, p. 12), so that the presence of wood borings in the digestive tract of *Teredo* is of itself no proof of utilization of wood as food. The principal constituents of wood, cellulose and lignin, are notoriously resistant to digestive action, so that they pass through the digestive tract of many animals entirely unchanged by the enzymes there present. *Teredo* is equipped to take its food from the water as do other lamellibranchs; also, the inner end of a teredo's burrow is often closed off by the formation of a shelly cross-partition, and the animal may live for an indefinite period with no contact with the wood whatever. Finally, wood that has passed through the digestive tract of the animal is shown by microscopic study to have retained its cellular structure (pl. 18, fig. 1), and some investigators even claim to have identified the kind of wood by its odor and color, as stated by Moll (1914, p. 526). This writer remarks that it is hardly conceivable that action on the wood by the digestive fluids should not have changed it more.

In reply to these arguments it may be said that *Teredo* is one of the most highly specialized of the boring mollusks, and might be expected *a priori* to differ from its rock-boring relatives in its method of obtaining nourishment. Some other types of animal are known to derive nutriment from wood, notably the termites (Banks and Snyder, 1920, p. 94) and various wood-boring beetles; among the mollusks, certain snails are known to secrete enzymes which act upon cellulose (Billard, 1914, p. 566). It would be surprising if *Teredo* were entirely to neglect so proximate a source of food as is afforded by the wood particles passing through its digestive tract. While the animal does sometimes partition itself off anteriorly from contact with the wood, it does not ordinarily do this until well grown, and probably not until forced to cease boring by the honeycombed condition of the wood. As regards the wood's retention of its physical properties after passage through the digestive tract, we may refer to König's observation (1913, p. 1101) that when cellulose is dissolved from wood by means of strong acids, the residual lignin still possesses the original woody structure. Hence we should expect that the appearance of the wood under the microscope would not be materially changed, even though the cellulose, hemicelluloses, and soluble sugars were entirely removed.

The most potent presumptive evidence in favor of the digestion of wood by *Teredo* is found in the anatomical structure of the digestive tract. The stomach opens posteriorly into an expanded and elongated blind sac, the caecum, in which the wood particles swallowed during boring operations are accumulated, being then periodically emptied into the intestine, whence they pass into the anal canal and are ejected through the dorsal siphon. It seems improbable that so specialized an organ as the caecum should have no significance in the economy of the animal except as a temporary storage place for extraneous sawdust on its way to the outside. The anatomical evidence on this point will be treated by Lazier in a paper shortly to appear in this series.

CHEMICAL CONSIDERATIONS

Indirect evidence, however, must of necessity be inconclusive. The need of definite experimental proof has suggested an approach to the problem from the chemical point of view. It should be possible to determine experimentally (1) whether or not the enzymes of *Teredo* are capable of acting upon any of the constituents of wood, or (2) whether or not the wood particles are chemically changed in their passage through the digestive tract.

The first of these alternatives has been selected for investigation by Harrington (1921), who has shown, though not so conclusively as might be desired, that a certain enzyme or enzymes extracted from excised livers of *Teredo norvegica* will act on sawdust to produce glucose. Since the liver extract failed to reduce pure cellulose, Harrington concludes either that the enzymes were not present in sufficient concentration, or that action on the wood was limited to hydrolysis of the hemicelluloses, which are notably more easily broken down than pure cellulose, with the further alternative that "there may be other substances present in wood which are necessary as co-enzymes to the ferment in question."

The present writers would suggest the possibility that the liver enzymes are not the only digestive ferments acting in the intestinal tract of *Teredo;* there may be enzymes from the crystalline style (Nelson, 1918, pp. 93, 107) or other parts of the digestive system, which are the necessary co-enzymes in the process of hydrolysis of wood. It is entirely within the limits of probability that a fluid capable of hydrolyzing cellulose may be poured out in the region of the foot, so as to serve the double purpose of softening the wood to facilitate boring and of preparing a part of it for absorption.

It is hoped that Harrington will press these interesting physiological investigations farther along the lines he himself has suggested. In the meantime, it has seemed to the present writers that very definite results might be obtained from the second method of investigation mentioned above, namely, by extracting and comparing the chemical constitution of the borings with that of the original wood, thus arriving at both a qualitative and quantitative determination of such changes as may take place during passage of the borings through the digestive tract.

Analysis of wood particles removed from the excised caecum would be open to criticism on more than one count. Aside from consideration of the almost impossible number of teredos that would be required for the accumulation of the necessary amount of the ingested wood, we are ignorant of the length of time the borings remain in the caecum before being ejected to the outside, and a great deal of the material thus secured might represent only the earliest stage of the digestive process; further, there is the possibility that some digestion takes place after the wood leaves the caecum, during its passage through the rather long intestine, especially the enlarged proximal portion, which contains a typhlosole. It seems extremely desirable that the material analyzed should be secured *after it has passed entirely through the digestive tract in normal fashion,* and been ejected through the excurrent siphon.

EXPERIMENTAL

At the marine laboratory maintained by the San Francisco Bay Marine Piling Committee on the Oakland mole of the Southern Pacific Railroad, through whose coöperation these studies have been made possible, for more than a year the writers have had under observation in aquaria a considerable number of *Teredo navalis*, which highly destructive species occurs locally in great numbers (Kofoid, 1921; Kofoid and Miller, 1922). The animals have continued boring and appear to thrive under conditions of aquarium life. From time to time wood borings were ejected in considerable quantities from the siphons (pl. 18, fig. 2). Such borings were carefully collected with a long pipette and dried. In about eight months sufficient material was accumulated by this method to permit of successful analysis.

Two aquaria, which we will term No. 1 and No. 2, supplied all the wood particles used. The original wood in both cases was Douglas fir, consisting in No. 1 of squared blocks planted in the bay for experimental infection and later placed in the aquarium, and in No. 2 of a section of piling infected at the time it was pulled. The material from the two aquaria has been kept separate and subjected to parallel analyses, as below described, thus rendering the results doubly significant.

The possibility was recognized of changes occurring in the composition of the wood subsequent to ejection, especially as it was not always possible to collect the borings with desirable promptness. In order to test the probability of such changes, some of the borings (series 1, sample 2) were allowed to remain on the bottom of the aquarium for about six months before being pipetted off.

The borings as collected were dried overnight at 100° C. in an electric oven, and crushed to pass a wire sieve having 50 meshes to the linear inch. Samples of the original wood were reduced to sawdust, then ground to pass through the 50-mesh sieve. To avoid changes in moisture content, all samples were preserved for analysis in tightly fitting glass stoppered bottles.

METHODS OF ANALYSIS

Analyses were made for moisture, ash, calcium, nitrogen, benzene extract, alcohol extract, reducing sugars in alcohol extract, hemicelluloses, cellulose, lignin, and furfural yield on distillation with hydrochloric acid. All these determinations were made on one sample of wood and the corresponding sample of ejected borings. On subsequent samples some of the determinations were omitted. Whenever possible determinations were made in duplicate, but in some instances the limited amount of available material made it necessary to depend upon single determinations.

1. *Moisture.*—One gram was dried for seventeen hours at 100° C. in a constant temperature electric oven.

2. *Ash.*—The dried material from the moisture determination was transferred to a platinum dish and incinerated over a wire gauze at a temperature below redness.

3. *Calcium.*—The ash was digested in dilute hydrochloric acid and the dissolved calcium estimated by precipitation as oxalate in slightly acid solution, and titration of the precipitate with permanganate. The conditions of precipitation were essentially those of McCrudden (1909).

4. *Nitrogen.*—Seven-tenths gram of material was treated by Gunning's modification of the Kjeldahl method. The results were calculated as protein by multiplying the nitrogen value by the factor 6.25.

5. *Benzene extract.*—One gram of the material was weighed out into an alundum extraction thimble and dried at 100° C. for several hours, then extracted for six hours in a Soxhlet apparatus. The benzene was evaporated off and the residue dried at 100° C. and weighed.

6. *Alcohol extract.*—The residue remaining in the thimble after the benzene extraction was extracted with 95 per cent alcohol for six

hours, the alcohol evaporated off and the residual extract dried at 100° C. and weighed.

7. *Reducing sugars in alcohol extract.*—The alcohol extract was digested in about 25 c.c. of hot water, allowed to cool, and basic lead acetate solution added until no further precipitation occurred. The precipitate was filtered off and the clear solution deleaded with sodium carbonate and filtered. The filtrate was neutralized with acetic acid, made up to 100 c.c. and reducing sugars determined by the Munson and Walker (1906) method, the cuprous oxide being burned to cupric oxide and weighed as such in the manner recommended by Davis and Daish (1913).

8. *Hemicelluloses.*—After the alcoholic extraction, the contents of the thimble were transferred to a 300 c.c. Erlenmeyer flask and hydrolyzed by digesting on the steam bath for three hours with 1 per cent hydrochloric acid, the conditions being those proposed by Spoehr (1919). The undissolved residue was filtered off and used for the cellulose and lignin determinations. The filtrate containing the hydrolyzed carbohydrates was neutralized with solid lead carbonate and after removing the lead precipitate and deleading, the reducing sugars were determined as described under "reducing sugars in alcohol extract."

Cellulose and lignin were determined upon separate portions of the residue remaining after the acid digestion for the removal of hemicelluloses.

9. *Cellulose.*—One portion of the residual material from the hemicellulose determination was transferred to a weighed Gooch crucible carrying a filtered disk of mercerized cotton cloth. Cellulose was then determined by the chlorination method of Sieber and Walter, which has been previously described by one of us (Dore, 1920*a*).

When this method was applied to the ejected borings, it gave a cellulose residue contaminated with a certain amount of non-cellulose material that resisted chlorination. To correct for the presence of this extraneous matter, the crude cellulose residue was weighed and the cellulose dissolved out of the mixture by digesting overnight in cold 72 per cent sulfuric acid. The mixture was diluted with water. The undissolved non-cellulose residue was collected on the original filter, washed, dried, and weighed. Its weight was deducted from the weight of crude cellulose previously obtained, thus giving the weight of true cellulose.

10. *Lignin.*—Another portion of the residual material from the hemicellulose determination was transferred to a 300 c.c. Erlenmeyer

flask, 10 c.c. of 72 per cent sulfuric acid added, and the whole allowed to stand overnight. The mixture was then diluted with 150 c.c. of water, heated to boiling and filtered on a Gooch crucible provided with a filtering disk of mercerized cotton cloth. The residue was washed thoroughly with hot water, dried in a glass stoppered weighing bottle for seventeen hours at 100° C. and weighed as lignin.

In order to learn whether the material obtained from the borings was actually lignin, it was submitted to alternate treatments with chlorine and 3 per cent sodium sulfite solution. The characteristic color reactions of lignin with chlorine and sulfite solution were given. The treatments were repeated until the sulfite solution was nearly colorless. Practically no residue then remained, indicating that the analytical product probably consisted entirely of lignin.

11. *Furfural yield on distillation with hydrochloric acid.*—One gram of the original material was treated by the method for pentosans described by the Association of Official Agricultural Chemists (1912).

Results

In tables 1 and 2 below are given the results of the analyses of wood and borings by these methods.

TABLE 1

Analyses of Wood and Borings: Series I

As found. All figures in percentages of air-dried material

Determination	Original Wood			Borings Sample 1			Borings Sample 2		
	Individual		Average	Individual		Average	Individual		Average
Moisture	4.89	4.91	4.90	7.36	....	7.36	7.31	....	7.31
Ash	8.42	8.02	8.22	24.17	....	24.17	30.66	....	30.66
Calcium in ash	0.62	0.68	0.65	0.66	....	0.66	....	....	....
Nitrogen	0.08	0.08	0.08	0.38	....	0.38	0.74	....	0.74
Protein (N×6.25)	....	....	0.50	....	....	2.27	....	....	4.62
Benzene extract	0.37	0.38		0.36					
	0.37	0.35	0.37	0.34	0.25	0.32	0.48	0.39	0.44
Alcohol extract	7.96	7.90		27.09					
	8.00	7.13	7.75	27.03	25.60	26.57*	....	....	....
Sugars in alcohol	0.33	0.32							
extract	0.44	0.32	0.35	0.09	0.15	0.12	....	....	....
Hemicelluloses	(4.20)†	5.32							
(as dextrose)	5.04	5.24	5.20	4.24	4.32	4.28	5.08	5.64	5.36
Cellulose	47.08	47.52	47.30	14.79	13.04	13.91	11.54	....	11.54
Lignin	26.47	26.41	26.44	36.11	....	36.11	32.13	....	32.13
Furfural yield	4.75	4.53	4.64	3.91	....	3.91	3.38	....	3.38

* Contains much NaCl. † Excluded from average.

TABLE 2

ANALYSES OF WOOD AND BORINGS. SERIES II

As found. All figures in percentages of air-dried material

Determination	Original Wood			Borings		
	Individual		Average	Individual		Average
Moisture	8.47	8.65	8.56	7.49	7.15	7.32
Ash	6.90	7.08	6.99	18.83	18.87	18.85
Nitrogen	0.14		0.14	0.70	0.72	0.71
Protein (N × 6.25)	0.87		0.87	4.38	4.50	4.44
Benzene extract	0.46 0.39	0.39 0.36	0.40	0.40 0.38	0.42 0.47	0.42
Sugars in alcohol extract	nil	nil	nil	nil	nil	nil
Hemicelluloses (as dextrose)	11.08 11.76	12.64 12.08	11.87	8.44	8.48	8.46
Cellulose	39.44	39.87	39.66	14.12	15.79	14.95
Lignin	23.63	22.91	23.27	38.16	37.71	37.93
Furfural yield	4.93		4.93	5.80		5.80

The purpose in determining moisture, ash, and protein was to enable us to reduce all data to a comparable basis. Since normal wood contains but small amounts of ash and protein, the amount found of these constituents may be taken as an approximate measure of the non-woody substances present in the samples. Accordingly, ash represents chiefly mineral contamination (shell fragments, salt, etc.) while protein represents animal remains.

The analytical figures for the respective wood samples and their corresponding borings are not directly comparable with one another since they are mixed with different amounts of non-woody material. In order to bring them to a common basis, the data have been recalculated to a moisture-free, ash-free, and protein-free basis. The results are given in table 3.

TABLE 3

RECALCULATION OF DATA OF TABLES 1 AND 2

	SERIES I			SERIES II	
		Borings			
	Wood	(1)	(2)	Wood	Borings
Moisture—plus ash, plus protein	13.62	33.80	42.59	16.42	30.61
Moisture-free, ash-free and protein-free material	86.38	66.20	57.41	83.58	69.39
DATA RECALCULATED TO MOISTURE-FREE, ASH-FREE, AND PROTEIN-FREE BASIS					
Hemicelluloses	6.02	6.46	9.33	14.23	12.19
Cellulose	54.74	21.01	20.10	47.45	21.54
Lignin	30.60	54.55	55.97	27.84	54.66
Furfural yield	5.37	5.91	5.89	5.90	8.36

The figures for benzene extract and alcohol extract appear to have no special significance. The former represents resinous matter, the latter tannins, coloring matter, and soluble sugars. None of these except the soluble sugars can be regarded as having any nutritive value for animals. The analyses show that extremely small amounts of soluble sugars are present in wood and borings. Accordingly, neither benzene soluble nor alcohol soluble constituents have been considered in the recalculations.

DISCUSSION OF RESULTS

The data show that each of the samples of ejected matter contains a much lower percentage of cellulose and a much higher percentage of lignin than the wood from which it was derived. The figures for hemicelluloses and furfural yield are less regular and not readily comparable on the basis given.

Inasmuch as it is extremely unlikely that any lignin was synthesized during the passage of material through the digestive tract of the animal, the increase in lignin is to be ascribed to concentration by removal of cellulose and other wood constituents. Assuming that the absolute amount of lignin remaining in the residue is the same as was in the original wood, we may calculate the percentage of the original wood substance remaining in each of the three samples of borings by determining in each case the ratio of the lignin content to that of the original wood. Thus the percentages of original wood substances in the samples of borings are:

$$\text{Series I, sample 1} \quad \frac{30.60}{54.55} \times 100\% = 56.1\%$$

$$\text{Series I, sample 2} \quad \frac{30.60}{55.97} \times 100\% = 54.7\%$$

$$\text{Series II,} \quad \frac{27.84}{54.66} \times 100\% = 50.9\%$$

The data of table 3 have been recalculated so that the constituents of the borings are expressed, not on 100 parts of borings, but on 100 parts of original wood, or, in other words, upon the number of parts of borings corresponding to the percentages found in the preceding paragraph. The results are given in table 4.

TABLE 4

DATA OF TABLE 3 CALCULATED TO PERCENTAGES OF ORIGINAL WOOD

Determination	Series I			Series II	
	Woods Parts per 100	Borings (1) Parts per 56.1	Borings (2) Parts per 54.7	Wood Parts per 100	Borings Parts per 50.9
Hemicelluloses	6.02	3.62	5.10	14.23	6.20
Cellulose	54.74	11.79	10.99	47.45	10.96
Lignin	30.60	30.60	30.60	27.84	27.84
Furfural yield	5.37	3.32	3.22	5.90	4.26

On this basis, it appears that during its passage through the animal's digestive tract the wood has lost about 80 per cent of its cellulose, and from 15 to 56 per cent of its hemicelluloses, including from 11 to 40 per cent of its furfural yielding constituents such as pentosans, etc.

The simplest explanation of this disappearance of carbohydrate material is that the cellulose and hemicelluloses of wood are partly digested by the teredo and probably hydrolyzed to simple carbohydrates which the animal can use as food. This view is consistent with Harrington's (1921) suggestion that the teredo contains enzymes capable of hydrolyzing cellulose; also with the results of Billard (1914), Bierry (1914), and Bierry and Giaja (1912), who have found cellulose-splitting enzymes in other mollusks.

The cellulose content and lignin content of the three samples of borings are remarkably uniform (see table 3). This would seem to indicate the composition of the residue which the teredo is incapable of digesting.

The experimental data rest upon the assumption that the analytical products, cellulose and lignin, are true to name. The results for the wood are based on well established methods (Dore, 1919, 1920) and may be accepted without question. In the case of the ejected matter, which is somewhat contaminated with animal remains, there might be some doubt as to whether the product after solution in 72 per cent sulfuric acid is actually lignin and whether the loss in weight which the chlorinated residue underwent really represents cellulose.

In order to determine the possibility of animal matter remaining undissolved by 72 per cent sulfuric acid and contaminating the lignin, the following experiment was performed: Several teredos were taken from the wood and the caeca dissected out and rejected, in order to eliminate the wood particles they contained. The flesh, thus freed from woody matter, was then dried and pulverized. The residue was digested overnight in cold 72 per cent sulfuric acid and then diluted in the same manner as in carrying out the lignin determination. Solution of the material was practically complete, showing that the presence of animal remains in the residue does not interfere with the lignin determination.

In the case of the cellulose, considerable difficulty was experienced in filtering and washing the material after the second chlorination. This appeared to be due to the presence of colloidal material in the mass. On dissolving out the cellulose from this residue by 72 per cent sulfuric acid, considerable amounts of insoluble substance were obtained, as shown by table 5.

TABLE 5

Cellulose Content of Wood and Borings

(Expressed in grams obtained from 1 gram of original material)

	Series I 1st sample of borings		Series I 2d sample of borings	Series II Sample of borings	
	(1)	(2)		(1)	(2)
Residue after chlorination	0.2620	0.2661	0.1420	0.2677	0.2714
Residue after acid digestion	0.1141	0.1357	0.0266	0.1265	0.1135
Cellulose by difference	0.1479	0.1304	0.1154	0.1412	0.1579

It is not believed that the insoluble residue contained a great deal of animal matter, as such material appears to be largely soluble in 72 per cent acid under the conditions employed. The residue is considered as consisting largely of lignin which escaped chlorination, due partly to the protective action of the colloidal mass and partly to the fact that the chlorination was not continued as long as usual on account of mechanical difficulties.

It is to be noted that the second sample of borings in Series I contains considerably more protein than the first sample of borings of the same series (see table 1). Nevertheless, it gave a much smaller yield of insoluble material in the cellulose determination, and the figures for cellulose and lignin were very similar to those from the other samples. This would tend to indicate that the methods used for cellulose and lignin are not affected by the amount of animal débris present in the sample.

It can be shown that, even if the analytical methods are seriously defective, the greatest possible allowance for contamination of products does not invalidate the general conclusion that the borings contain a considerably smaller proportion of cellulose to lignin than the wood from which they were derived. If the cellulose figure is low, the correct value can in no case be higher than the total residue after chlorination (see table 5) and if the lignin is high, due to contamination with animal remains, the correct value can in no case be lower than the lignin value given minus the total protein of the sample. From tables 1, 2, and 5 we can then calculate the following:

	SERIES I Borings		SERIES II Borings
	(1)	(2)	
Maximum possible value for cellulose	26.40	14.20	26.95
Minimum possible value for lignin	33.84	27.51	33.49

In every case, the cellulose is materially less than the lignin, whereas in the original wood the cellulose is about twice as much. It appears impossible, therefore, to draw from the data any other conclusion than that the cellulose partly disappears during digestion.

We have previously referred to the possibility that the change in the composition of the wood may occur after the material is ejected by the borer. The compositions of the first and second samples of borings in Series I furnish some experimental evidence on this point. Although the second sample was purposely left in the sea water for at least six months longer than the first, there was no significant reduction in carbohydrate constituents (see table 3). In view of the extreme resistance of wood to purely chemical action, and the absence of known cellulose-destroying fungi or bacteria in sea water, it seems more reasonable to ascribe the loss of cellulose and other carbohydrates to digestive action while in the body than to external agencies.

Plankton is doubtless the principal food of *Teredo* as of other lamellibranchs, and on account of its high protein content is probably very suitable for purposes of growth and repair of waste. The teredo which is boring, and consequently growing to fill the larger cavity, requires, besides the protein food to provide for growth, a considerable additional amount of food to furnish energy for its boring activities. This energy could be supplied by the protein material of the plankton, but much more efficiently by carbohydrates, inasmuch as these last are completely oxidized and there is therefore no necessity of getting rid of nitrogenous products. If, then, when its boring activities are greatest, the teredo has available a considerable supply of carbohydrate material to furnish the necessary energy and that available in proportion to the amount of work to be done, it appears to be a most natural arrangement, admirably adapted to its needs. The carbohydrates of the wood therefore play an important part in supplying the teredo with energy when it is most needed.

It does not appear probable that *Teredo* could subsist over any long period upon the wood alone, because of the negligibly small amount of protein material. Especially during boring would considerable nitrogenous matter be required. The need for a simultaneous supply of plankton is accordingly indicated.

If the conclusion is accepted that wood tissue is partly digested and absorbed as food by *Teredo*, some light is thrown upon the probable mechanism by which toxic substances injected into the timbers of marine structures protect against teredo attack. If partial digestion of wood occurs, it is clear that all substances contained in the wood must experience an intimate contact with the teredo's digestive fluids over a considerable period of time. Optimum conditions then prevail for the absorption of toxic substances and their effectiveness is limited only by such factors as lack of solubility, inability of their solutions to penetrate the walls of the digestive tract, etc., these factors being dependent upon the properties of the agent and not upon the condition of exposure. No case of failure of a given toxin to protect can be ascribed to physical isolation of the borings as we might expect if the wood were regarded as wholly undigested and merely mechanically handled by the teredo.

These considerations offer practical suggestions in regard to (1) the commercial preservative treatment of marine timbers, and (2) the testing of the toxicity of preservative substances. We may conclude that the established practice of preserving marine timbers by impregnating the wood with toxic substances is a rational and efficient process for introducing these substances into the animal's system, for it is clear that the teredo cannot bore into the wood without being exposed to the action of any toxins that are capable of entering through its digestive tract. As to methods of carrying out toxicity tests, it would appear that those methods which use the wood as a vehicle for carrying the toxin possess a distinct advantage over methods in which the toxin is introduced into the animal by some other means, on account of the greater certainty that contact with the digestive juices will occur.

In conclusion, the authors wish to acknowledge, and express their thanks for, helpful suggestions which they have received from

members of the Advisory Committee appointed by the University of California to coöperate with the San Francisco Bay Marine Piling Committee.

SUMMARY

1. It has long been a debatable question whether or not the boring mollusks of the genus *Teredo* exercise any digestive action on the wood particles which are swallowed during boring and retained for a time in the caecum before being passed to the outside. The absence of any conclusive evidence has suggested an experimental approach to the problem.

2. A chemical analysis has been made of three samples of wood borings ejected by *Teredo* and of two samples of the original wood from which the borings were derived.

3. The results indicate that the wood loses about 80 per cent of its cellulose and 15 to 56 per cent of its hemicelluloses during its passage through the digestive tract of *Teredo*.

4. The carbohydrates which disappear are probably utilized as food by *Teredo*.

5. The woody portions of the ejected material have a uniform composition of about 21 per cent cellulose and 55 per cent lignin. Possibly this represents the ultimate residue which the animal is unable to digest.

6. The digestible carbohydrates in the wood may play an important rôle in the economy of *Teredo* in supplying energy for its boring activities, supplementing the plankton diet upon which it mainly depends for growth and repair.

7. Digestion of wood constituents by *Teredo* produces optimum conditions for the absorption of toxic substances contained in the wood.

8. Impregnation of wood is an efficient method of introducing toxins into the borer's system, either for commercial preservation of the wood or for testing experimentally the protective action of toxins, because of the assured contact between toxin and digestive fluids.

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EXPLANATION OF PLATE

PLATE 18

Fig. 1. Wood borings ejected by *Teredo,* magnified 300 diameters. Observe that in many of the particles the cell walls are visible.

Fig. 2. Siphons protruding from blocks of wood containing *Teredo.* Photographed in aquarium, natural size. The long siphons are the incurrent ones. The excurrent siphons are relatively short, usually protruding only two or three millimeters from the openings of the burrows. Note ejected wood borings around many of the openings.